

Grazing and spring snow counteract the effects of warming on an alpine plant community in Tibet through effects on the dominant species

Tsechoe Dorji^{a,b,*}, Kelly A. Hopping^{c,d}, Shiping Wang^{a,b}, Shilong Piao^{a,b}, Tenzin Tarchen^e, Julia A. Klein^{d,f}

^a Key Laboratory of Alpine Ecology and Biodiversity, Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Nongke Road No. 6, Lhasa, 850000, Tibet Autonomous Region, China

^b CAS Center for Excellence in Tibetan Plateau Earth Science, Campus 16 Lincui Road, Chaoyang District, 100101, Beijing, China

^c Human-Environment Systems, Boise State University, Boise, ID 83725, USA

^d Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO 80523, USA

^e Institute of Grass Sciences, Academy of Agriculture and Animal Husbandry of Tibet Autonomous Region, Lhasa, 850000, Tibet Autonomous Region, China

^f Department of Ecosystem Science and Sustainability, Colorado State University, Fort Collins, CO 80523, USA

ARTICLE INFO

Keywords:

Tibetan Plateau
Community properties
Field experiment
Species richness
Species evenness
Species diversity

ABSTRACT

Although studies have investigated the independent effects of warming, snow, and grazing on alpine plant community properties – including plant species richness, evenness, and diversity – the interactive effects of these climate and grazing factors have not been addressed experimentally in cold systems. We investigate the effects of these climate change and grazing factors using 5 years of data collected from a relatively long-term (2009–2015), fully-factorial field experiment in an alpine meadow ecosystem on the central Tibetan Plateau. Specifically, we investigate: 1) how experimental warming, spring snow addition, and yak grazing independently and interactively affect plant community properties, including diversity metrics and relative contributions of different plant life forms to the total plant cover, and 2) how the changes in plant community properties are associated with the proportional cover of the dominant plant species, *Kobresia pygmaea* within the total vegetation cover. We found that warming reduced species richness and increased species evenness and the proportional cover of shrubs within the total vegetation cover. Snow addition also increased species evenness. Grazing increased the proportional cover of *K. pygmaea* within the total vegetation cover, while decreasing that of grasses. Grazing also counteracted warming-induced increases in shrubs. Treatment-induced changes in *K. pygmaea* cover were strongly correlated with the indices of plant community properties and were generally in the opposite direction of changes in species evenness and diversity. We conclude that the projected increases in spring snowstorms and maintaining moderate levels of grazing can counteract some warming effects on the plant community. Moreover, the performance of the dominant species can regulate plant community responses to climate change and livestock grazing on the central Tibetan Plateau.

1. Introduction

Global mean temperatures have been increasing exponentially since the pre-industrial period, with alpine and arctic systems experiencing an even stronger magnitude of warming than lowland and temperate regions (IPCC, 2013). Warmer temperatures and more frequent extreme weather events are projected to occur across the Tibetan Plateau (Christensen et al., 2013; He et al., 2016; Jiang et al., 2012; Yang et al., 2012). The Tibetan Plateau encompasses approximately 1.2 M km² of semi-arid alpine grassland (Zhang et al., 2014), equivalent to 0.9% of

Earth's total terrestrial land area (Coble et al., 1987), and is among the most vulnerable eco-regions to climate warming (IPCC, 2013). Episodic extreme snowstorms represent one of the key types of extreme events on the Tibetan Plateau that is expected to increase (Jiang et al., 2012; Shen et al., 2015; Wang et al., 2018). Extreme snowstorms can have devastating effects on livestock and livelihoods (Klein et al., 2011), but the ecosystem effects of snowstorms, and their interactions with warming and grazing, have not been explored. Within the semi-arid alpine grassland eco-region, the alpine meadow ecosystem is one of the dominant ecosystem types on the Tibetan Plateau, covering more than

* Corresponding author at: Key Laboratory of Alpine Ecology and Biodiversity, Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Nongke Road No. 6, Lhasa, 850000, Tibet Autonomous Region, China.

E-mail addresses: tsechoedorji@itpcas.ac.cn, tssechoedorji@qq.com (T. Dorji).

<https://doi.org/10.1016/j.agrformet.2018.08.017>

Received 14 December 2017; Received in revised form 20 August 2018; Accepted 21 August 2018

Available online 31 August 2018

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one-fourth of its total vegetated land surface (Wang et al., 2016), and supporting more than two-thirds of the total livestock population on the Tibetan Plateau according to local official statistics. Livestock grazing is the primary type of land use and has been hypothesized to be the main driver of the formation of alpine meadow ecosystems on the Tibetan Plateau (Miehe et al., 2011b).

The interacting impacts of climate change and livestock grazing on alpine grassland plant communities, including aspects such as species richness, evenness, and composition, are evident on the eastern margin of the Tibetan Plateau (Klein et al., 2004; Wang et al., 2012). The resulting changes in plant community properties can affect ecosystem functioning and the provision of services, such as forage for livestock production (Avolio et al., 2015; Hopping et al., 2018; Ma et al., 2017) and soil carbon sequestration (Chapin et al., 2000; Hopping et al., 2018). However, the complexity of factors mediating plant community responses to interacting global change drivers further underscores the need for more multi-factorial experiments (White et al., 2014). Studies that consider multiple, interacting factors have led to key system insights, including the finding that experimental warming effects on plant community composition are mediated by grazing (Klein et al., 2004; Post and Pedersen, 2008), soil moisture availability (Xu et al., 2016) and permafrost status (Yang et al., 2018). Yet, no arctic or alpine warming studies to date have directly manipulated temperature, grazing and moisture inputs (including extreme events). Understanding the independent and interactive effects of these drivers is essential, particularly for grazed ecosystems such as the Tibetan Plateau, where not only are temperatures increasing, but where the timing and amount of precipitation are also projected to change (Christensen et al., 2013; He et al., 2016; Wang et al., 2018), and where grazing policy changes are also underway (Bauer and Nyima, 2011).

A dominant plant species can exert a strong influence on plant community properties due to its high proportional cover, which is mainly the result of being highly adapted to the local biotic and abiotic conditions (Grime, 1998; Kardol et al., 2010; le Roux et al., 2013). Competition from the dominant species may reduce species richness and evenness, whereas release from competition with the dominant species may allow other species to increase, thereby increasing richness and evenness (Cerabolini et al., 2010). Dominant species may play a significant role in community productivity, by, for example, counterbalancing large declines in rare and uncommon species (Smith and Knapp, 2003), and/or in community composition, by, for example, inducing competitive exclusion of subdominant species under warming if warmer conditions favor highly competitive dominant species over subordinate ones (Olsen et al., 2016). Therefore, understanding the ways in which changing temperatures, precipitation, and land use will affect the dominant species will be important for predicting how plant communities as a whole will respond to climate and land use changes (Kardol et al., 2010). This understanding is particularly important for alpine meadow grasslands on the Tibetan Plateau, where the dominant species, *Kobresia pygmaea* C. B. Clarke, is both highly palatable for livestock and resistant to grazing (Miehe et al., 2008). Moreover, it is also a shallow-rooted, early-flowering sedge species that is sensitive to upper-soil moisture availability, which could be altered by climate change (Hu et al., 2013).

Thus, the objectives of our study were to quantify:

- 1) How growing-season warming, simulated spring snowstorms, and yak grazing independently and interactively affect plant species richness, evenness, diversity, and proportional vegetation cover of different plant life forms (sedges, grasses, forbs, and shrubs).
- 2) How the variation in plant species richness, evenness, diversity, and the proportional vegetation cover of different plant life forms relates to changes in proportional vegetation cover of the dominant plant species under experimental manipulations.

We hypothesized that experimental warming during the growing

season will decrease plant species richness due to non-random species loss (Cross and Harte, 2007) or local extinction (Walker et al., 2006), but that this effect will be dampened by growing-season yak grazing, due to grazers' ability to counteract community composition shifts under warming in other alpine and arctic systems (Klein et al., 2004; Post and Pedersen, 2008). We also hypothesized that spring snow addition will increase plant species richness, evenness, and thus diversity, because the increase in soil moisture availability with snow addition can promote emergence, growth, and population expansion of shallow-rooted, early flowering, rare species in semi-arid ecosystems (Dorji et al., 2013; Porporato et al., 2001). Finally, we expected that yak grazing will promote *K. pygmaea* dominance, given its adaptations to grazing as discussed above.

2. Materials and methods

2.1. Study design

This study was conducted in a semi-arid, alpine meadow grassland near Nam Tso Lake, central Tibet, China (30.72°N, 91.05°E, 4875 m a.s.l.). The grassland is dominated by *K. pygmaea*. There are also commonly occurring sub-dominant plant species, such as *Potentilla saundersiana* Royle, *Potentilla bifurca* Linn., *Potentilla fruticosa* Linn., *Carex moorcroftii* Falc. ex Boott, and *Astragalus rigidulus* Benth. (Fig. S1). In total, we found 53 vascular plant species – including 7 sedges, 37 forbs, 7 grasses, and 2 shrubs – in our experiment across all years and treatments.

Mean annual air temperature was -0.71°C , while mean air temperature in winter (December 1–February 30) was -9.59°C , in summer (June 1–August 30) was 8.43°C , and during the growing season (May 1–September 30) was 5.93°C , as measured by a nearby weather station from 2006 to 2017 (NAMORS, 2018). The mean annual precipitation was 407 mm, but this mainly falls during the summer monsoon season from June to September (NAMORS, 2018). Winter snowfall is typically low in this region and sublimates quickly, primarily due to strong solar radiation and wind at this elevation, leaving the vegetation snow-free during much of its dormant season. However, episodic, severe snowstorms do occur, and these are projected to increase in frequency and severity (Jiang et al., 2012; Shen et al., 2015; Wang et al., 2018). The Plateau is also simultaneously undergoing climate warming at rates above the global mean (IPCC, 2013; Wang et al., 2008) and is projected to face up to an additional 2.0°C of warming by 2035 and 4.9°C by 2100 under the RCP4.5 scenario, along with up to a 25% increase in winter precipitation (Christensen et al., 2013), which is expected to fall as snow.

We conducted this study using a factorial study design with three factors (growing season warming – “warming” hereafter, spring snow addition – “snow addition” hereafter, and growing season yak grazing – “yak grazing” hereafter), fully crossed to yield 8 treatments (warming, snow addition, yak grazing, warming + snow addition, warming + yak grazing, snow addition + yak grazing, warming + snow addition + yak grazing, and control without warming, yak grazing, or snow addition). Each of the eight treatments was assigned to 8-m diameter plots in a randomized block design (Fig. S2a). This randomized block design was used to account for topographic and potentially edaphic variability in the study area – specifically along the hillslope and with distance from the adjacent streambed. This resulted in eight blocks, each containing one replicate of each of the eight treatments, for a total of 64 plots. Note that we originally had 16 treatment combinations, which included pika exclusion for half of the eight blocks. However, the pika treatment was ineffective (Dorji et al., 2013; Hu et al., 2013), and we did not attempt to exclude pikas from any part of the experiment after 2012, thus we did not include pika effects in our data analyses.

We established the treatments starting in June 2009 (Dorji et al., 2013; Hu et al., 2013). Each plot contained five permanent, systematically-located, 1-m-diameter subplots (Fig. S2a). Although we treat

subplots as representative of their larger plot analytically, it was logistically necessary to use multiple subplots within a plot to (a) keep disruptive sampling and infrastructure (i.e., microclimate monitoring equipment) out of the long-term vegetation monitoring subplots, and (b) to make the warming and snow addition treatments more tractable, while also allowing yaks sufficient space to graze across a larger area. Thus, we applied the warming and snow treatments to each of the five 1-m diameter subplots that were within the 64 8-m diameter plots assigned to each of these treatments, while yak grazing occurred across the full extent of the 8-m plots.

We used ITEX (International Tundra Experiment) open top chambers (OTCs) to achieve warming conditions in the study (Dorji et al., 2013; Walker et al., 2006). Although OTCs have drawbacks due to being a passive warming system, they are nonetheless the only tractable option for a long-term study in a remote location far from the nearest power supply, which is key for free air warming facilities (Kimball et al., 2010). The conical OTCs are made of Sun-Lite HP fiberglass (Solar Components Corporation, Manchester, New Hampshire, USA) and are 1.5 m in diameter at the base, 0.75 m in diameter at the top, and 0.4 m tall (Fig. S2b). We erected the OTCs immediately after the added snow melted each year. We elevated the OTCs approximately 5 cm above the ground to allow air circulation and small mammals within the OTCs. From 2009 to 2013, we left the OTCs on the plots until at least August 24 and no later than September 3 due to logistical reasons, but we left them on until October 10th in 2014 and October 14 in 2015 to cover the entire growing season. We conducted the warming treatment only during the growing season, rather than year-round, for several reasons. First, our experiment was initially designed to be comparable with ITEX studies that were primarily simulating summer/growing season warming scenarios in alpine and arctic regions across the northern hemisphere (Cha et al., 2005; Elmendorf et al., 2012a, b). In addition, it was also necessary to remove the OTCs to prevent excessive wind and hail damage to them during the harsh winter, as well as to avoid the confounding effects of ambient snow capture or exclusion by the chamber walls.

Each year since 2009, snow was applied to the subplots in mid- to late April, before the onset of green-up for most plant species (Dorji et al., 2013; Hopping, 2015). Snow was collected from snow banks close to the study site, where snow accumulated in naturally occurring depressions sheltered from wind. This was then shoveled into temporary wire frames that were placed around each of the subplots to contain the snow. The snow additions were approximately 1-m in diameter and 0.5-m in height (Fig. S2c). The mean amount of snow added to the snow treatment plots each year was equivalent to 279 ± 42 mm of water (mean \pm 1SD, $N = 110$ plots, measured 2009–2013) (Hopping, 2015). The experimental snow addition was approximately equivalent to 1.22 m (\pm 0.18 sd) of naturally falling, fresh snow (Hopping, 2015), which is within the range of large ‘snow disaster’ snowstorms reported for this region (Li et al., 2001). Added snow remained on the plots for 8.4 days on average.

The yak grazing treatment was applied in three sessions in 2010–2012 and 2015 (in June, July, and August), in two sessions in 2014 (in July and August) and in one session in 2009 and 2013 (in mid-July), due to logistical constraints. During each grazing session, local herders tethered 1 yak per grazing plot for three days, for approximately 7 h each day (Fig. S2d). Air sensors (see the next section for more details) and OTCs located within grazing plots were removed during the time when yaks were present in the experiment in order to avoid damage to the infrastructure and to allow yaks free access to graze the plots. To estimate grazing off-take rate, we recorded the location of yak-grazed patches (differentiated from pika herbivory) and measured their area and vegetation height within a sampling quadrat (0.75×0.75 m) after each grazing session. By comparing newly grazed patches to the previous grazing record within individual subplots, we were able to isolate new off-take that occurred during each session. Then, we applied an area-height-biomass regression to estimate grazing

off-take rate based on the measured volume of the grazed patches (Hopping, 2015). The off-take rates in our grazing treatment were similar to those of ambient grazing that we measured outside the experiment (~ 5.25 g m⁻²) in our study area.

2.2. Data collection

We used Decagon ECT, 5TM and EC-TM sensors and EM50 loggers (Decagon Devices, Pullman, Washington, USA) to measure air temperature at 10-cm aboveground and soil temperature and moisture at 10-cm belowground within one of the five subplots that was designated for instrumental measurements in each plot. We calibrated the dielectric moisture data to our field soils to obtain volumetric soil water content. Measurements were logged every 15 min for all sensors. We used data from May 25 to August 25 each year (2010, 2011, 2012, 2014, and 2015) to estimate growing season mean microclimate conditions (air and soil temperature and soil moisture) for each plot in each year. We removed abnormal microclimate values that were due to sensor malfunction. Then, if a plot was missing more than 8 consecutive days of microclimate data, we excluded it from calculations of growing season means to prevent it from unintentionally skewing the results.

Plant community properties were measured in a sampling quadrat (0.75×0.75 m) placed in one of the five 1-m subplots within each of the 64 8-m-diameter plots in mid-August each year, when most of the plants had reached maximum growth. The subplots in which these measurements were made were designated as non-destructive subplots, meaning that they were not used for any destructive sampling or equipment installations throughout the entire duration of the experiment. We treat them as representative of the larger plots in which they are located. To ensure that these measurements were performed in the same location each year, we placed the sampling quadrat in the center of the subplot, with its corners mounted on fixed metal pegs. The quadrat frame was evenly divided by nylon monofilament into 400 grid cells.

From 2010–2012 we visually estimated the areal cover of species within each of the grid cells. The areal cover measurements included species that comprised at least 1/6 of the area of a cell. Species in a subplot that were never large enough to meet this criterion were recorded separately as being present from 2014 to 2015, we recorded the presence/absence (“1”/“0”) of each species within each of the grid cells. In 2014, we only recorded species frequency data within 100 grid cells (the 0.75×0.75 m quadrat frame was evenly divided into 100 grid cells) due to a shortage of labor. Neither the areal cover nor presence/absence methods distinguished among individuals, given the difficulty in doing so for *K. pygmaea*’s turf-like growth. This ocular-based estimate provides higher probability in detecting more species than point-intercept methods (Godínez-Alvarez et al., 2009). To make the 2010–2012 measurements comparable to those from 2014 to 2015, we converted the areal cover data to presence/absence data by assigning “presence” (“1”) to every species with some cover in each grid cell. The total number of presences for each species within each subplot was then equivalent to the total number of grid cells that contained that species. Species that were present in a subplot but did not meet the minimum area criterion in 2010–2012 were assigned a “1” for that subplot. Due to logistical constraints, different data collection techniques were used in 2009 and 2013, thereby precluding us from incorporating comparable cover estimates for those years.

We divided the total number of presences for each species by the total number of presences for all species found in a subplot to obtain an estimate of the proportional cover of each species relative to the total vegetation cover in each subplot every year. By estimating proportional cover data in this way, we are able to assess the contribution of each species to the vegetation community as a whole. However, we note that this is not an indication of species’ absolute cover, since it only accounts for cover relative to other vegetation and not to the total surface area of the sampling quadrat.

We also used the presence/absence data to calculate plant species richness, evenness, and diversity in each subplot every year. Species richness was defined as the total number of species found within each subplot. We calculated species evenness and the Simpson's diversity indices using the statistical program PAST (Hammer et al., 2001). We chose to use the Simpson's diversity index (diversity, hereafter), because it is reported to perform better over other diversity indices when dominant species/traits are expected to be important in the community (Morris et al., 2014).

We also calculated the proportional vegetation cover of different plant life forms (other sedges, forbs, grasses, and shrubs) by summing the proportional vegetation cover of all species belonging to each life form, with *K. pygmaea* excluded from the "other sedges" life form group.

2.3. Analyses

We used analyses of variance (ANOVA) based on generalized linear mixed effects (GLME) models to test the effect of treatments (warming, snow addition, and yak grazing), year (2010, 2011, 2012, 2014, 2015), and their interactions on the following response variables: species richness, evenness, diversity, the proportional vegetation cover of *K. pygmaea* (dominant plant species), other sedges (non-*K. pygmaea* sedges), grasses, forbs, shrubs, and sub-dominant plant species. We also used Analyses of Covariance (ANCOVA) based on GLME models to test how the dominant species (*K. pygmaea*) effect on response variables changes under different treatments and in different years. We used GLME models to analyze the direction and magnitude of treatment effects on corresponding response variables. We used "Block" and "year" as random effects in the GLME models when only treatment effects were a primary concern, in order to account for unintended variation among "blocks" as well as repeated measures across years. We used a poisson distribution with a log link function in GLME models when response variables were count data (i.e., species richness), and a binomial distribution with a logit link function when response variables were proportional (i.e., proportional cover of vegetation life forms). We performed contrast analyses by using the same GLME model structure with intercepts (the reference for the comparison) specified differently among treatments. We did so in order to keep the original model structure in the contrast analyses, instead of using means-based differences among treatments. We report the effects of warming, snow addition, yak grazing and their interactions on each response variable relative to the corresponding non-warming, non-snow addition, and non-yak grazing subplots, unless specified. We consider the subplots as representative of the larger plots in which they are embedded, and since

we did not conduct vegetation or microclimate measurements across multiple subplots within a plot for this study, we refer to them simply as "plots" hereafter.

All the analyses were performed in R i386 3.4.4 (R Development Core Team, 2012), and GLME models were performed using the "glmmadmb" function in the "glmmADMB" package for GLMEs (Fournier et al., 2012). We used this function because it can account for excessive zeros in response variables (by setting "zeroInflation = TRUE"), which was necessary for analyses of proportional cover of some vegetation groups, such as grasses and shrubs.

3. Results

3.1. Treatment effects on microclimate conditions

During years with vegetation measurements, warming significantly increased mean growing season air temperatures ("air temperature" hereafter) by 1.19 °C, on average, and mean growing season soil temperatures ("soil temperature" hereafter) by 1.82 °C, on average. Warming significantly decreased mean growing season soil moisture ("soil moisture" hereafter) by 4.03%, on average, relative to control plots (Table S1; Fig. S3a, b, and d). Yak grazing did not affect air or soil temperatures, but it did interact with warming to reduce soil moisture relative to plots without warming or grazing (Table S1; Fig. S3c). Snow addition significantly reduced the effects of warming on soil temperature, but did not fully restore soil temperatures to un-warmed levels (Fig. S3e). Across all years, snow addition significantly increased average monthly soil moisture in April, May, and June relative to plots without climate manipulations (Fig. S4). By July and August, soil moisture in plots with snow addition was no longer different from those without snow additions or warming. However, in plots with warming, those that also received snow additions maintained significantly higher soil moisture throughout the entire growing season.

3.2. Treatment effects on the plant community

3.2.1. Species richness

The mean species richness in control plots was 13.52 (± 0.47 SE), while the maximum number of species in a single plot was 24. Warming decreased species richness by 13% (1.6 species) on average, relative to un-warmed plots, across all years. The significant, interactive effects of warming and yak grazing indicate that grazing reduced species richness relative to un-warmed and un-grazed plots, but did not promote a further decrease in warmed plots beyond that occurring with warming alone (Table 1; Fig. 1a). Snow addition did not significantly affect

Table 1

Results of analyses of variance (ANOVA) based on generalized linear mixed effect (GLME) models showing the effects of warming (W), snow addition (S), yak grazing (G), year, and their interactions on species richness, evenness, Simpson diversity index, and on the proportional vegetation cover of *Kobresia pygmaea*, other sedges (without *Kobresia pygmaea*), grasses, forbs, and shrubs in the experiment. Blocks were assigned as a random variable in analyses. Degrees of freedom (df) and test statistics (F) are shown, and significant effects are indicated by *** ($P < 0.001$), ** ($P < 0.01$), * ($P < 0.05$).

	df	Richness	Evenness	Diversity	<i>Kobresia pygmaea</i>	Other sedges	Forbs	Grasses	Shrubs
W	1, 273	29.92 ***	4.1*	1.23	1.55	6.35 *	53.87 ***	0.61	26.64 ***
S	1, 273	2.64	10.10 **	0.59	2.39	12.22 ***	1.68	0.93	0.13
G	1, 273	2.37	16.74 ***	14.90 ***	13.63 ***	4.18 *	0.06	80.52 ***	0.35
Year	4, 273	26.34 ***	62.28 ***	17.90 ***	21.38 ***	0.67	36.73 ***	8.44 ***	3.42 **
W × S	1, 273	0.97	4.44 *	0.19	0.82	6.27 *	1.86	0.75	2.22
W × G	1, 273	4.04 *	5.27 *	0.13	0.39	5.00 *	12.73 ***	0.21	18.17 ***
S × G	1, 273	0.31	0.29	0.49	0.82	0.21	0.01	0.23	6.41 *
W × Year	4, 273	1.57	6.02 **	1.80	2.08	0.16	3.46 **	0.74	0.65
S × Year	4, 273	0.84	0.64	0.05	0.04	0.48	0.22	1.51	0.07
G × Year	4, 273	0.83	1.34	0.20	0.25	0.20	0.34	0.87	0.07
W × S × G	1, 273	1.23	0.57	1.65	1.13	13.02 ***	5.88 *	0.08	1.19
W × S × Year	4, 273	0.42	0.70	0.42	0.42	0.07	0.17	0.53	0.10
W × G × Year	4, 273	0.20	0.10	0.04	0.04	0.18	0.14	0.29	0.16
S × G × Year	4, 273	0.07	0.17	0.09	0.13	0.00	0.20	0.69	0.12
W × S × G × Year	4, 273	0.08	0.08	0.08	0.12	0.17	0.36	0.35	0.06

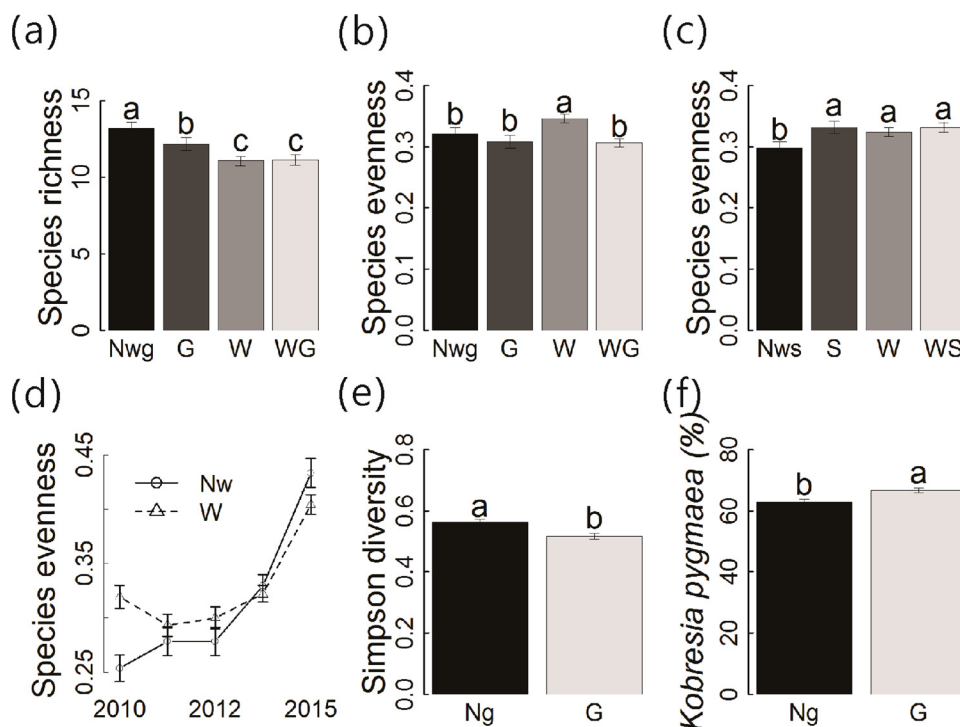


Fig. 1. Results of analyses of variance (ANOVA) based on generalized linear mixed effect (GLME) models showing the significant effects of growing season warming (W), spring snow addition (S), yak grazing (G), and their interactions on species richness (a), evenness (b–d), Simpson diversity index (e), and the proportional vegetation cover of *Kobresia pygmaea* (f) in the experiment. Blocks were assigned as a random variable in analyses. Error bars are ± 1 standard error. Different letters above the bars indicate significant differences among treatments. Other Abbreviations: Nwg = No warming or yak grazing; Nws = No warming or snow addition; Ng = No yak grazing.

species richness independently or in interaction with other factors (Table 1).

Warming, snow addition, and yak grazing affected forb species richness through significant, two-way interactions. Warming and snow additions each caused a significant loss of forb species, but these losses were mitigated when yak grazing was also present, and were completely reversed under the snow addition \times yak grazing treatment (Table S2, Fig. S5a, S5b). Warming effects on forb species richness varied significantly among years, with a significant decrease in forb species richness under warming in 2010 and 2012, but no significant effect in 2011, 2014, and 2015 (Table S2; Fig. S5c). By contrast, yak grazing significantly reduced grass species richness (Table S2, Fig. S5d). Yak grazing and snow addition each caused a significant increase in sedge species richness, but this increase was reversed by the interaction of grazing and snow addition (Table S2, Fig. S5e). There were no significant three-way interactions among warming, snow addition, and yak grazing that affected the species richness of any plant life form (Table S2).

3.2.2. Species evenness

Warming interacted significantly with both yak grazing and snow addition in its effects on species evenness across all years (Table 1). Yak grazing reduced the warming-induced increase in species evenness to a level that was no longer significantly different from un-warmed plots (Fig. 1b). Warming, snow addition, and their interaction each increased species evenness across all years, but the significant interaction of warming and snow addition did not further enhance the independent effects of warming and snow addition on species evenness (Fig. 1c). Warming effects on evenness also varied significantly among years, with a significant increase in evenness under warming in 2010, no significant effect in 2011–2014, and then a significant decrease in evenness under warming in 2015 (Table 1; Fig. 1d). There were no significant interactive effects between snow additions and yak grazing, nor between all three factors, on species evenness (Table 1).

3.2.3. Species diversity

Yak grazing decreased species diversity, regardless of whether snow and/or warming was also added (Table 1; Fig. 1e). By contrast, neither

warming nor snow addition had any significant effects on species diversity (Table 1). Warming, yak grazing, and snow addition together did not interactively affect species diversity across all years (Table 1).

3.2.4. Dominant species

Yak grazing increased the proportional contribution of *K. pygmaea* to the total vegetation cover (*K. pygmaea* cover, hereafter) regardless of whether warming or snow were also added (Table 1; Fig. 1f). Neither warming nor snow addition had any significant effects on *K. pygmaea* cover across years, either independently or in interaction with other factors (Table 1).

3.2.5. Other sedges

Warming, snow addition, and yak grazing interactively affected the proportional contribution of other sedges – not including *K. pygmaea* – to the total vegetation cover (“other sedge cover” hereafter) across years (Table 1, Fig. 2a). Other sedge cover decreased under yak grazing alone without climate manipulations, whereas warming and snow addition each independently increased other sedge cover, regardless of whether yak grazing was also present. The interactive effects of warming and snow addition further increased other sedge cover to a level that was significantly higher than that of warming or snow addition alone. However, the three-way combination of warming, snow addition, and yak grazing reduced the promoting effects of warming and snow addition on other sedge cover to a level that no longer differed significantly from that of control plots.

3.2.6. Forbs

Warming, snow addition, and yak grazing also interacted to significantly affect the proportional contribution of forbs to the total vegetation cover (“forb cover” hereafter) across years (Table 1, Fig. 2b). Warming independently decreased forb cover, and the addition of either snow or yak grazing did not significantly alter this effect. However, the combination of snow addition and yak grazing, with or without warming, recovered forb cover to a level no longer significantly different from that of control plots. The effects of warming on forb cover also varied significantly across years, with no significant effect due to warming in 2010, but with more significant decreases in subsequent

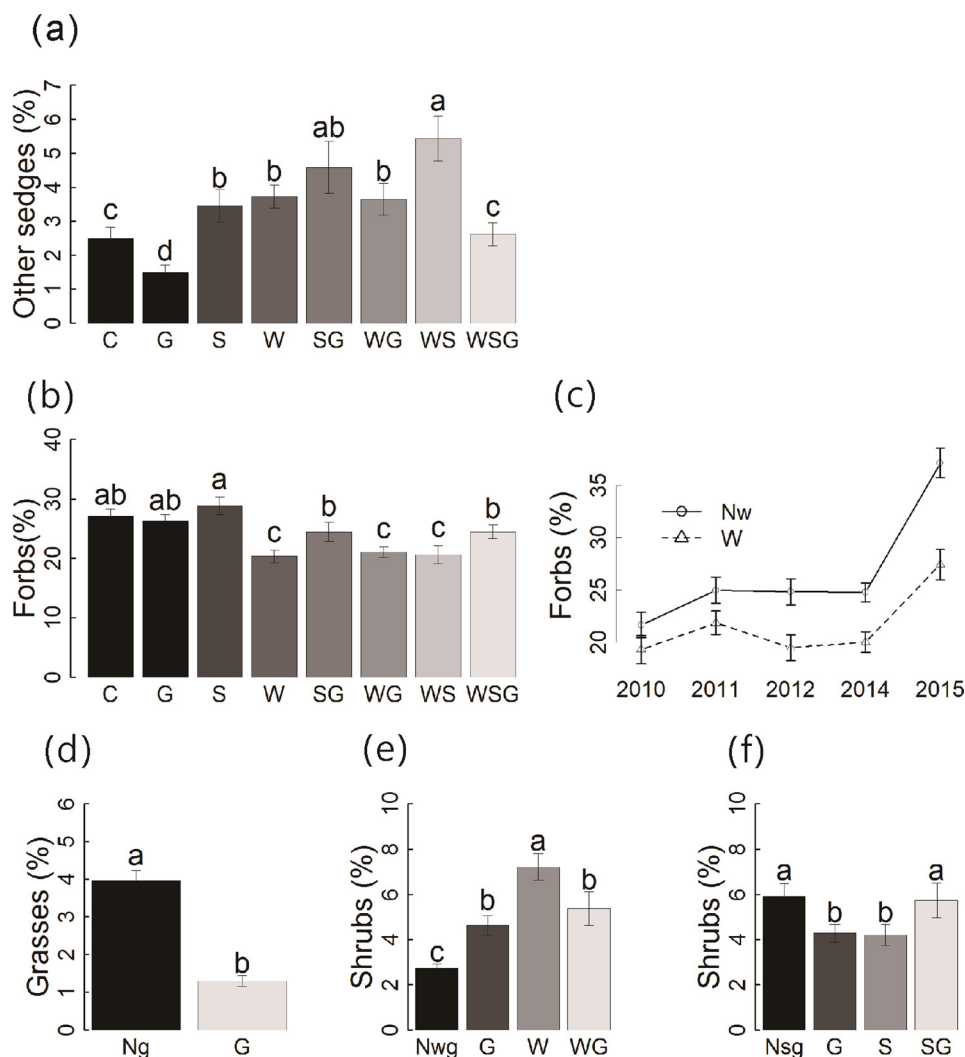


Fig. 2. Results of analyses of variance (ANOVA) based on generalized linear mixed effect (GLME) models showing the significant effects of growing season warming (W), spring snow addition (S), yak grazing (G), and their interactions on proportional vegetation cover of other sedges (excluding *Kobresia pygmaea*) (a), forbs (b and c), grasses (d) and shrubs (e and f) at Nam Tso, central Tibet. Blocks were assigned as a random variable in analyses. Bars are ± 1 standard error. Different letters above bars indicate significant differences among treatments. Other Abbreviations: Nwg = No warming or yak grazing; Nsg = No snow addition or yak grazing; Ng = No yak grazing.

years (Table 1; Fig. 2c).

3.2.7. Grasses

Yak grazing significantly decreased the contribution of grasses to the total vegetation cover (“grass cover” hereafter), regardless of other treatments and across all years (Table 1; Fig. 2d). Neither warming nor snow addition significantly affected grass cover independently or in combination with any other treatment factors.

3.2.8. Shrubs

Warming increased the proportional contribution of shrubs to the total vegetation cover (“shrub cover” hereafter) across years (Table 1; Fig. 2e). However, there was a significant warming and yak grazing interaction whereby grazing reduced the promoting effect of warming on shrub cover. Snow addition and yak grazing also interactively increased shrub cover when compared to subplots with either snow addition or yak grazing alone (Table 1; Fig. 2f). The three-way interaction of warming, snow addition, and yak grazing did not significantly affect shrub cover (Table 1).

3.3. Relationships among community properties and the dominant species

Across all treatments and years, plant species richness, evenness, and diversity decreased significantly as the proportional vegetation cover of the dominant species, *K. pygmaea*, increased (Table S3; Fig. 3). These negative associations between plant community properties and *K.*

pygmaea cover were maintained under warming, snow addition, and yak grazing independently (Fig. S6). *K. pygmaea* cover explained 99% of variation (adjusted R^2) in species diversity and 46% of variation in evenness, but only 19% of variation in species richness, across all treatments and years (Fig. 3a, b, and c).

The proportional cover of other sedges, forbs, grasses, and shrubs also decreased significantly as *K. pygmaea* cover increased across all treatments and years (Table S3; Fig. 4), and these negative associations between other plant life forms and *K. pygmaea* were maintained under warming, snow addition, and yak grazing independently (Fig. S7). *K. pygmaea* cover explained 35% of variation in other sedge cover, 41% of variation in forb cover, 18% in grass cover, and 24% in shrub cover across all treatments and years (Fig. 4a, b, c, and d).

The proportional contribution of sub-dominant species to the total vegetation cover decreased significantly as the proportional cover of *K. pygmaea* increased (Fig. S8). *K. pygmaea* cover explained 23% of the variation in *P. fruticosa* cover, 12% in *P. suandersiana* cover, 7% in *P. bifurca* cover, 22% in *C. moocroftii* cover, and 9% in *Leontopodium pusillum* (Beauv.) Hand.-Mazz. cover across all treatments and years. The only species that we tested that was not significantly affected by changes in *K. pygmaea* cover was *Astragalus rigidulus* Benth, a sub-dominant legume.

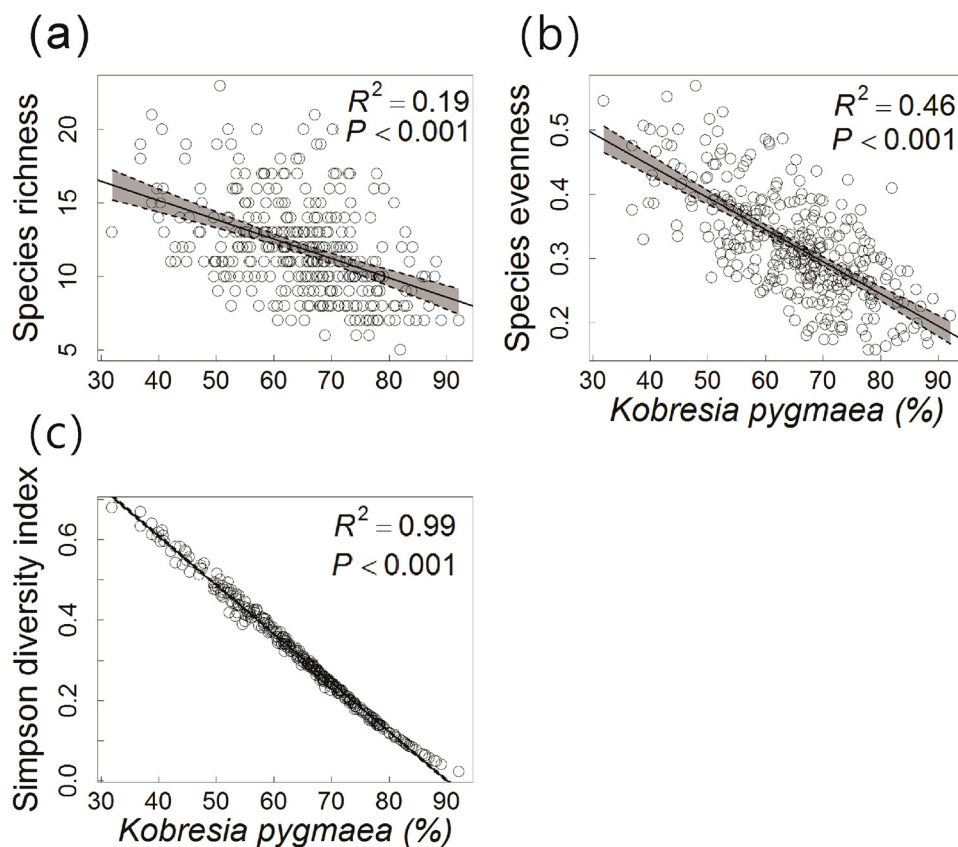


Fig. 3. Linear relationships between plant species richness (a), evenness (b), and Simpson diversity (c) with the proportional vegetation cover of *Kobresia pygmaea* across years and treatments in the experiment. Adjusted R^2 and p-values are provided. Transparent gray areas between the two dashed black lines indicate 95% confidence intervals.

4. Discussion

4.1. Decreases in species richness under warming are driven by a decrease in forbs

We found that warming decreased plant species richness, as

reported elsewhere (Klein et al., 2004; Shi et al., 2015; Walker et al., 2006; Wang et al., 2012). The warming-induced reduction in species richness could primarily be attributed to the warming-driven reduction in forb species in our study, despite the finding elsewhere that forb species can respond individually to warming (Cross and Harte, 2007; Klein et al., 2007). Warming manipulations in our study also

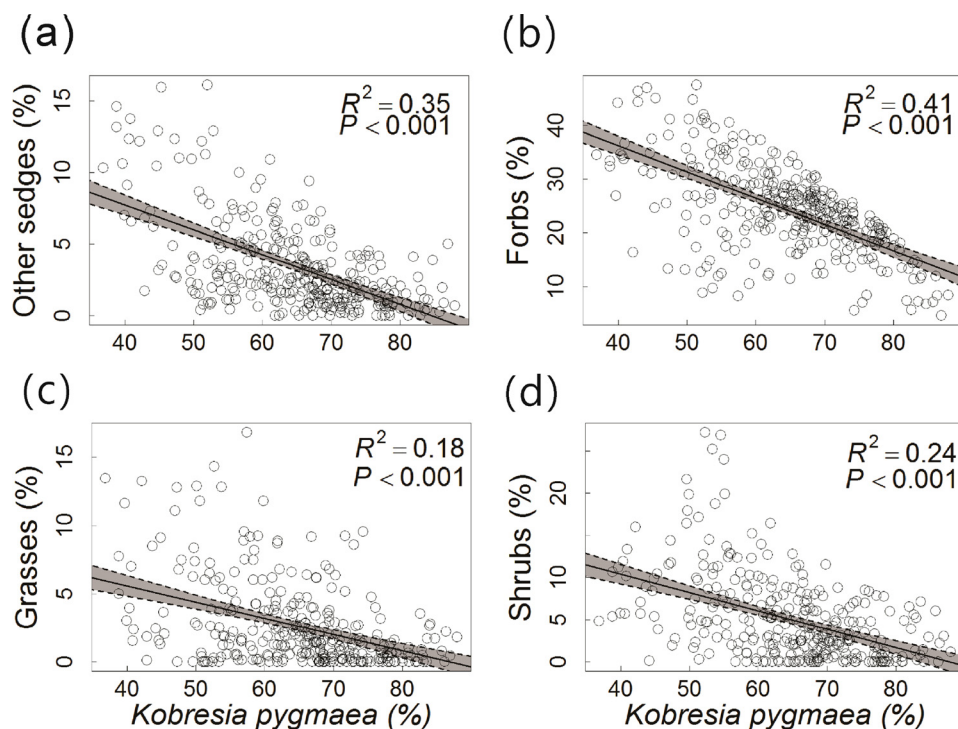


Fig. 4. Linear relationships between the proportional vegetation cover of other sedges (excluding *Kobresia pygmaea*) (a), forbs (b), grasses (c) and shrubs (d) with proportional cover of *Kobresia pygmaea* across years and treatments in the experiment. Adjusted R^2 and p-values are provided. Transparent gray areas between the two dashed black lines indicate 95% confidence intervals.

caused a significant reduction in soil moisture in upper soil layers, which may limit growth and population expansion of plant species, particularly those that are sensitive to water availability (Porporato et al., 2001). The forb life form comprises a total of 37 species in our experiment – five times more species than the number of grasses or sedges. Thus, there was a higher probability of obtaining more drought-sensitive forb species, which may remain dormant or disappear due to warming-induced upper soil moisture limitation, than the other life forms we examined.

While warming caused significant reductions in the number of forb species and their proportional cover, neither grass nor sedge species richness, nor grass proportional cover changed significantly under warming. A grass species in the experiment, *Stipa purpurea* Griseb., dominates drier alpine steppe grasslands, and *C. mocroftii*, the second-most abundant sedge species in our study plots, dominates sandy grasslands, a transitional stage between alpine steppe and alpine desert, across the northwestern Tibetan Plateau (Miehe et al., 2011a). These biogeographical patterns indicate that these grass and sedge species are likely more tolerant of drier conditions, and so warming-induced water limitation in the experiment had little effect on them, or even increased the proportional cover of *C. mocroftii* (Fig. S1b). The two shrub species in our study are both deeper-rooted and are thus capable of utilizing deeper soil water without being as influenced by soil surface water conditions (Hu et al., 2013). Together, these results indicate that warming can reduce the abundance and proportional cover of drought-sensitive forb species in these alpine meadows, which in turn causes a reduction in total plant species richness.

4.2. Spring snow addition increased species evenness due to other sedges

While species richness and diversity did not change under snow addition, there was a significant increase in species evenness, which was likely primarily due to other sedges, since snow addition increased other sedges, but did not affect forb, grass, or shrub cover in our study. Our study system is a semi-arid, water-limited system (Hopping, 2015). While added snow did not change average soil moisture availability for the entire growing season, it did significantly increase soil moisture in April, May and June, the months just prior to the start of the monsoon season. Thus, the snow-induced increase in soil moisture during these dry months could benefit plants, particularly the shallow-rooted, early emerging species that mostly utilize upper-soil water during the pre-monsoon season in our study area (Hu et al., 2013) and/or those that are opportunistic when there is a favorable condition (Körner, 2003; Moreno-Gutierrez et al., 2012), such as *C. mocroftii*, the dominant species within the other sedge life form that increased its cover under snow addition.

However, snow addition did not increase the proportional cover of *K. pygmaea*, an early-emerging sedge, and instead caused a non-significant reduction in *K. pygmaea* cover. This is surprising, because our earlier studies showed that *K. pygmaea* also uses upper soil moisture during the pre-monsoon season, and that snow addition advances the date of inflorescence production for *K. pygmaea*, as well as increasing its mean number of inflorescences (Dorji et al., 2013; Hu et al., 2013). Nor did we detect an interaction between snow addition and year on *K. pygmaea* cover, which indicates that the effects of snow addition on *K. pygmaea* did not differ among years. The relative stability of *K. pygmaea* in response to snow addition could be following patterns reported elsewhere, which found that dominant plant species were more temporally stable than less abundant species under environmental perturbation (Ma et al., 2017), and that phenological shifts were more rapid than were changes to other traits in response to climate change scenarios (Cleland et al., 2006). Or other factors, such as nutrient availability, may have prevented *K. pygmaea* from responding positively to the higher soil moisture available under the snow addition treatment. Nevertheless, since *K. pygmaea* was the most dominant plant species, comprising 64% of the total vegetation cover, it is likely that even the

non-significant decrease in *K. pygmaea* cover under snow addition could have reduced competition for other species that were either opportunistic (Körner, 2003; Moreno-Gutierrez et al., 2012) or sensitive to upper-soil moisture availability during the pre-monsoon season (Hu et al., 2013).

4.3. Grazing is an intrinsic system property for maintaining *K. pygmaea*-dominated alpine meadows

Grazing is the primary type of land use in central Tibet and has been hypothesized to be the main driver behind the formation of alpine meadow ecosystems on the Tibetan Plateau (Miehe et al., 2011b). Moderate grazing can enhance biological diversity (Grime, 1973), and grazing can mediate the effect of warming on plant species richness (Klein et al., 2004), composition (Post and Pedersen, 2008), and biomass (Kaarlejärvi et al., 2013). In our study, yak grazing did not significantly affect plant species richness, but decreased evenness, diversity and the proportional cover of grasses, while increasing the proportional cover of *K. pygmaea*. The decreased species evenness and diversity under moderate yak grazing was unexpected according to the intermediate disturbance hypothesis, which predicts that moderate levels of disturbance should enhance species diversity in a community (Grime, 1973; Milchunas et al., 2008; Roxburgh et al., 2004). However, this unexpected result can be attributed to the increase in the proportional cover of *K. pygmaea* under yak grazing, because *K. pygmaea* is a grazing-tolerant species that is highly palatable and a good-quality forage (Miehe et al., 2011b). The reduction in grass cover under yak grazing, however, could be mainly due to grasses' high palatability and upright growth form that make them easy targets for grazing, thereby causing the reduction in grass species richness and grass cover under grazing. These results imply that ambient grazing can maintain or even enhance the dominance of *K. pygmaea* in alpine meadows, and thus the ability of the rangelands to support pastoral livelihoods on the Tibetan Plateau. This finding also supports the ecological theory that for systems that evolved with a long history of grazing, the removal of grazing is a disturbance, just as fire suppression in a fire-adapted system can lead to severe changes in the structure and functioning of that system (Milchunas and Lauenroth, 1993).

4.4. Novel insights from a three-factor experiment

Two-way interactive effects of warming and yak grazing showed that yak grazing mediated the effects of warming on plant species evenness and shrub expansion, which is consistent with findings from the northeastern Tibetan Plateau (Klein et al., 2007). This interaction between climate change and land use factors has important implications for the future structure and functioning of these grasslands under warming, depending on the extent to which livestock continue to graze these systems.

Our study also demonstrated that spring snow addition altered the effect of warming on soil temperature and pre-monsoon soil moisture, and also caused an increase in species evenness. Summer warming and winter snow accumulation experiments conducted at Niwot Ridge, Colorado and Toolik Lake, Alaska showed a complex response of different plant species (Walker et al., 1999) and an altered species composition after 20 years (Leffler et al., 2016), while a similar study conducted in a Mediterranean alpine area indicated that snow accumulation is expected to mitigate warming temperatures by acting as a barrier against colonization of thermophilous species (Abeli et al., 2012). Both of these studies indicate that there are strong effects of two-way treatment interactions on plant community properties and population dynamics.

The novel finding from our three-factor experiment is that the combined effects of grazing and snow maintained compositional and life form characteristics even under warming. These results further imply that continued ambient grazing and projected increases in

snowstorms may mediate the effects of warming on plant community properties in the alpine meadow grazing ecosystem in this region, specifically by controlling shrub expansion, forb loss, and *K. pygmaea* dominance. However, the projected addition of spring snow will not occur every year and will continue to be episodic (albeit more frequent), and, importantly, can also have direct, devastating impacts on livelihoods (Klein et al., 2011). Since grazing is an intrinsic system property in our study area, as discussed above, changes in livestock management policies, which include fencing to ensure boundaries for grazing rights for communities or even households, as well as limits to livestock numbers per individual pastoralist as a means of controlling carrying capacity on rangelands (Bauer and Nyima, 2011), will thus also affect plant communities, as shown in our study. These changes in plant community properties could further alter ecosystem functioning and services (Avolio et al., 2015; Chapin et al., 2000; Ma et al., 2017).

4.5. Impacts of the dominant species on plant community properties and dynamics

Our findings highlight the key role of plant species interactions that are indicated by the significant, negative associations among plant species richness, evenness, and diversity and the proportional vegetation cover of *K. pygmaea*. Although warming did not significantly affect the proportional cover of *K. pygmaea* as measured in this study, our previous findings that warming significantly delayed *K. pygmaea*'s reproductive phenology, reduced its number of inflorescences (Dorji et al., 2013), and caused significant dieback in the first years of the experiment (Hopping et al., 2018) suggests that warming decreases the performance of *K. pygmaea*, the most dominant plant species, thereby causing a reduction in competition for other co-occurring species (Cerabolini et al., 2010; Hopping et al., 2018). Sub-dominant species that are more drought-tolerant and persistent under warming could be particularly well positioned to take advantage of this reduced competition from *K. pygmaea*, and a transition to a more shrub-dominated landscape (Hopping et al., 2018) or more steppe-like vegetation composition could be likely consequences of warming-induced *K. pygmaea* loss. Changes in species composition have also been observed under both short- (Klein et al., 2007) and long-term (Zhang et al., 2017) warming and grazing manipulations on the eastern margin of the Tibetan Plateau and elsewhere (Dornelas et al., 2014; Harte and Shaw, 1995; Shi et al., 2015), as has the role that the dominant plant species can play in structuring plant community composition (Klein et al., 2004) (Harte and Shaw, 1995; Olsen et al., 2016; Smith and Knapp, 2003). Our study also indicates that the proportional cover of all but one of the most abundant, sub-dominant plant species was higher when the proportional cover of *K. pygmaea* decreased. Competition for resources—particularly for the nitrogen supply that is limited in alpine meadow grasslands on the Tibetan Plateau (Niu et al., 2006)—from *K. pygmaea* could be less effective than *A. rigidulus*, because it is a legume species that is capable of fixing atmospheric nitrogen (Christiane et al., 2008). However, the other species that we examined here do not have nitrogen-fixing properties, thus might be more prone to resource competition from *K. pygmaea*. These results again indicate that interactions among co-occurring species are important for regulating plant community properties and that the direction and magnitude of changes in *K. pygmaea* cover under warming can significantly alter plant community properties and thus ecosystem functioning in the region.

5. Conclusion

Taken together, the results of this study indicate that (i) maintaining moderate levels of grazing and projected increases in snowfall may mediate the effect of climate warming on plant community properties in the alpine meadow grazing ecosystem on the Tibetan Plateau, in large part through their effects on *K. pygmaea*; and (ii) the performance of the dominant plant species, *K. pygmaea*, in response to changes in

climate and land use will regulate plant community structure and composition, and thus influence the ecosystem's ability to provide vital functions and services, such as forage for livestock production.

Author contribution

K.A.H. and J.A.K. designed the experiment; T.D., K.A.H., and J.A.K. conducted the experiment; T.D., K.A.H., and T.T. collected data; T.D. wrote the manuscript; T.D., K.A.H., J.A.K., S.P., and S.W. jointly discussed and provided critical input on the manuscript throughout the writing process. All authors gave final approval for publication.

Conflict of interest

The authors declare no conflict of interest.

Acknowledgements

This work was jointly supported by the National Natural Science Foundation of China (31770524 and 31470524) awarded to T.D.; Key Research program of Tibet Autonomous Region of China awarded to S.W.; NSF-USA #SBE-0624315 awarded to J.A.K.; NSF-USA Graduate Research Fellowship and NSF-USA #OISE-1015691 awarded to K.A.H.; and the National Natural Science Foundation of China (41230750, 31272488), Programs from Strategic Priority Research Program (B) of the Chinese Academy of Sciences (XDB03030403), and National Basic Research Programs of China (2013CB956000) awarded to S.W.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.agrformet.2018.08.017>.

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